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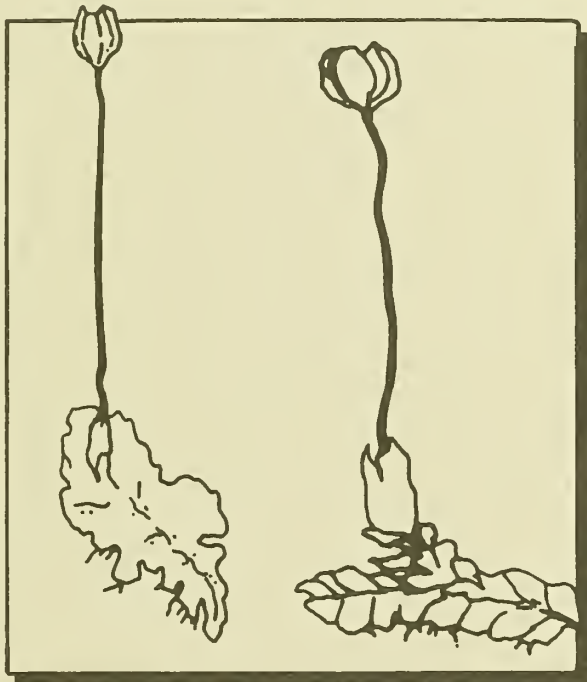Experiment Station

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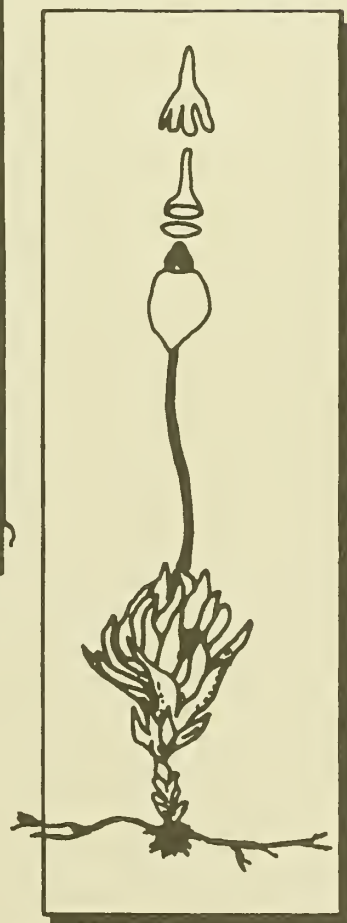
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Terrestrial Cryptogams of Pinyon-Juniper Woodlands in the Southwestern United States: A Review

Juanita A.R. Ladyman and Esteban Muldavin

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Abstract. Terrestrial cryptogams are comprised of algae, lichens, mosses, fungi, and liverworts. Because they are small and inconspicuous, they are commonly overlooked, yet they are important components of pinyon-juniper ecosystems of the Southwest. Terrestrial cryptogams provide soil structure, reduce soil erosion, contribute to nutrient cycling, and enhance nutrient status and ecosystem productivity. Cryptogamic cover helps preserve biological diversity and provides suitable habitat for certain endemic plants. Cryptogams also have the potential to contribute to medical discoveries and other commercial uses. Some crusts are dominated by algae, others by lichen and moss. There is evidence that cryptogams occupy land that would otherwise be bare in pinyon-juniper communities. Research results do not support the belief that cryptogamic crusts compete with grass and other vascular plants. Fire and grazing are destructive to crusts. Grazing, especially during dry conditions, has been shown to cause long-term damage to crusts. Research is needed for alternative grazing strategies that lessen the impact and help sustain cryptogamic crusts and their associated benefits in the ecosystem. Technology to inoculate land to encourage recolonization by cryptogams is being developed. After disturbance, natural recolonization by algae can be relatively rapid (within five years) although mosses and lichens are relatively slow to recover (15-100 years). This review of the literature indicates that there is a substantial amount of quantitative evidence, both causal and correlative, that supports the premise that cryptogamic crusts perform important ecological functions, parto ticularly with respect soil stabilization and nutrient cycling in the Southwest. More multi disciplinary research would be advantageous. Management of cryptogamic crusts is complex because of long recovery times and the potential for species loss following disturbance. Long-term sustainable management of pinyon-juniper woodland will require careful consideration of the role cryptogams play in the ecosystem. It is probable that cryptogam life forms will feature more prominently in land managers' ecosystem management strategies.

Keywords: cryptogams, woodland management, microphytic crusts, pinyon, juniper

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OVERVIEW

A cryptogamic crust is a brown, black, grey, or white soil-cover composed of either algae, lichen, moss, fungi, or liverwort, alone or combined. These organisms are frequently overlooked because of their small size and neutral color. Another term for cryptogamic crust is microphytic or biotic crust, which includes bacteria, diatoms, and fungal spores that are part of the microscopic component of the cryptogamic crusts. This review discusses the visually observable algal, lichen, moss, and liverwort components of crytogamic crusts; however, the terms cryptogamic, microphytic and biotic crust are interchangeable in this report.

Living, crytogamic crusts should not be confused with inorganic desert crusts frequently called "crusts" by soil scientists and geologists (e.g. Watson 1989; Lancaster and Nickling 1994). During dry periods, cryptogam crust formed by cyanobacteria (blue-green algae) appears similar to a soil crust formed by raindrop impact (Booth 1941; Isichei 1990). Rain-induced soil crust reduces water infiltration, and increases runoff and erosion. In contrast, the cryptogam crust minimizes erosion and provides nitrogen to the soil (Fletcher and Martin 1948; Harper and Marble 1988).

Previous reviews on cryptogamic crusts include ones by Harper and Kimball (1988), Klopatek (1991), and West (1990). This review focuses on research results from studies on the form and function of terrestrial cryptogams in pinyon-juniper woodland and woodland savannas in the Southwestern United States, which include New Mexico, Arizona, Colorado, Utah, and Nevada. The soil and vegetation variation in Southwestern pinyon-juniper ecosystems is extensive and com-

plex (Gottfried 1991). Therefore, this review also addresses related communities, such as those dominated by black brush (*Coleogyne ramossissima*) and big sage (*Artemisia tridentate*).

Data from other parts of the world are described if relevant to the cryptogams of the Southwest. All papers cited are in English, German, or French. Generally, scientists from the former Soviet Union believe that cryptogams are undesirable ecosystem components (West 1990). Some literature in the United States suggests that cryptogamic crusts are undesirable and should be broken up by hoof action (e.g., Savory 1988). Gutknecht (1991) describes them as "ecological frosting" implying that they have a trivial role in the ecosystem. Articles that reject the ecological function of cryptogams often rely on qualitative assessments rather than quantitative measurements and analysis (e.g., Savory 1988; Gutknecht 1991). They also often discount evidence contrary to their opinion as the result of poorly designed experiments (Gutknecht 1991).

Others view terrestrial cryptogams as significant ecosystem components. They contribute to landscape stability and increasing nutrient status and biodiversity (Johansen 1986; Harper and Kimball 1988; Klopatek 1991) by reducing soil erosion, contributing to the biomass, and increasing the available nitrogen (Harper and Kimball 1988) in a nitrogen- and carbon-deficient soil (Gottfried 1991). As information is accumulated, land managers will be able to consider cryptogam life forms when planning a sustainable ecosystem management strategy. Our purpose is to provide a comprehensive overview of the status and environmental role of cryptogamic crusts in the Southwestern United States.

PINYON-JUNIPER WOODLAND

Pinyon-juniper (PJ) woodlands are often referred to as pygmy forests due to the relatively small stature of these conifers. PJ woodland occupies the zone between the more arid ecosystems (desert shrub, chaparral, or semi-arid grassland) of the lower elevations and the more mesic, higher elevation ponderosa pine forest.

PJ woodland is prominent in the Southwestern United States with 90 percent of its range in New Mexico, Colorado, Utah, and Arizona (Mexal et al. 1991). Juniper dominates at lower elevations and pinyon at higher elevations. The species composition of both pinyon and juniper changes between regions. *Pinus edulis* (doubleleaf pinyon) occurs throughout the range. In extreme southwestern Utah, northwestern Arizona, and to the west, *Pinus monophylla* (single leaf pinyon) replaces *P. edulis* at lower elevations. In southwestern New Mexico and southeastern Arizona, Mexican pinyon (*P. cembroides*) is also found. *Juniperus deappeanna* (alligator juniper) is prominent in southeastern Arizona and west-central New Mexico. *Juniperus oesteosperma* (*J. utahensis*; Utah juniper) is dominant in Utah, northern Arizona, and western Colorado. *Juniperus monospermae* (one-seed juniper) is the primary species southeastward into Arizona and New Mexico. *Juniperus scopulorum* (rocky mountain juniper) is the major species east of the continental divide in Colorado and at higher elevations. At their range boundaries, Juniper species are associated with one another but in differing abundances.

The growing season in PJ woodland is April to October. Annual precipitation varies from 12 inches at lower elevations to about 18 inches in areas where PJ woodland merges into ponderosa pine forest. At higher elevations, the PJ woodland is characterized by a closed-canopied woodland dominated by pinyons. The undergrowth is commonly shrubby with low-growing oaks (*Quercus gambelii*, *Q. pauciloba*, and *Q. turbinella*), or mountain mahogany (*Cercocarpus montanus*). In contrast, the lower elevations are dominated by junipers forming open-canopied savannas with grasses (e. g., *Bouteloua* sp., *Oryzopsis hymenoides*, *Hilaria jamesii*) dominating the broad, intertree spaces. This savanna is a transition zone between the woodlands of the higher elevation rugged montane areas, and the grasslands of the lowland Great Plains, Great Basin, and Chihuahuan Desert (Dick-Peddie 1993). In the Great Basin region these open stands are dominated by shrubs such as Bigelow sagebrush (*Artemisia bigelovii*) or shad scale (*Atriplex confertifolia*), rather than grasses.

Overall, there is a significant diversity of communities in the PJ woodland. In the Western United States, over 100 plant species have been identified as growing in PJ woodland (Bourgeron and Engelking 1994). Dick-Peddie (1993) recognized 36 community types in New Mexico alone. Because of the wide distribution, PJ woodland communities grow on a wide variety of soils, parent materials, and landforms. The soils tend to be alkaline, well drained, shallow, rocky, and infertile. Because of the low annual precipitation, rough topography, and soil features, using irrigation to increase productivity is not possible (Dortignac 1960; Gottfried 1991; Mexal et al. 1991). Research on cryptogams in PJ woodlands centers on open-canopied communities with grassy or bare intertree spaces. The terrain in these locations is more gentle than the montane communities.

PJ woodland provides important wildlife habitat (Swenson 1977), but large herds of year-round heavy grazing animals, such as bison, did not evolve with the PJ woodland vegetation west of the Rockies (Platou and Tueller 1985). Instead, areas occupied by PJ woodlands were winter range for relatively small bands of ungulate browsers such as pronghorn antelope, deer, and big horn sheep (Mack and Thompson 1982).

Other than wildlife habitat, the uses of PJ woodlands are varied. Commercial activities range from production of specialty items such as pinyon nuts and Christmas trees, to forage production for livestock and extensive fuel wood cutting. PJ woodland is also used for recreational activities such as hiking, camping, and bird watching.

PJ woodlands contain many watersheds (Watershed Management Practices for Pinyon Juniper Ecosystems 1992). Although water quantity may not significantly increase through management (Dortignac 1960), its quality, and ultimately its usable quantity, may decrease through poor management (Watershed Management Practices for Pinyon-Juniper Ecosystems 1992). Therefore, although the water quantity from PJ woodland watersheds is relatively small (Dortignac 1960), considering the state of the long

term water supply in the western United States (Graf 1988; Van Schilfgaarde 1991), it may become the most important commodity that PJ woodland supplies.

CRYPTOGAM BIOLOGY

Early botanists misunderstood the reproductive mechanisms of fungi, algae, and bryophytes; they cataloged them together in one class called Cryptogamia. The word cryptogam refers to plants that reproduce by spores rather than seeds. Cryptogams are subdivided into lower cryptogams, (algae and fungi) and higher cryptogams (ferns and their allies, *Lycopodium*, *Equisetum, and Selaginella),* which are often called vascular cryptogams. Although this review focuses on the lower cryptogams (unicellular algae, cyanobacteria, lichens, mosses and liverworts), Selaginella and ferns are in PJ woodlands and, *Selaginella* especially, may help stabilize the soil surface (Ladyman and Muldavin 1994a). Also, remember that all cryptogamic crusts include microscopic bacteria, diatoms, and fungi along with the lichen/algal/moss component.

Algae

Algae are simple photosynthetic organisms with a unicellular or multicellular body called a thallus, which can be a filament, flattened or ribbon-like. Algae is not a formal taxon and species are separated into different divisions based on structure, flagella (a long thread-like projection from a cell that is used for motion) morphology, chemical nature of the cell wall, assimilatory products (such as carbohydrates), and pigments. The divisions are: Bacillariophyta (diatoms), Charophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanophyta, Euglenophyta, Phaeophyta, Pyrrophyta, Rhodophyta, and Xanthophyta. Many alga owe their common names to the pigments they contain. Among the most abundant terrestrial algae are the Cyanophyta (blue-green algae), Chlorophyta (green algae), and Xanthophyta (yellow-green algae).

Cyanobacteria (blue-green algae) are uniquely able to both photosynthesize and fix nitrogen.

Nitrogen fixation involves the conversion of atmospheric nitrogen to ammonia, which is the first step in protein synthesis. The process is inhibited by oxygen but blue-green algae have specialized cells (heterocysts) with thick walls that exclude oxygen. The nitrogenase enzyme, which is the enzymic catalyst for the conversion of nitrogen to ammonia, is in these heterocysts. Energy is required for nitrogen fixation whether it occurs in the light using photosynthate (a product of photosynthesis), or in the dark using stored carbohydrates (Kershaw 1985).

Almost all algae in terrestrial crusts have a sheath and are mobile (Campbell 1979). Cyanobacterial sheaths (external layer that surround the filaments) and mucilages (a gelatinous substance that contains protein and polysaccharides) are believed to act as water reservoirs during dry periods to slow dehydration. Although moisture is important, algal growth also depends on temperature. A study in PJ woodlands by Johansen and Rushforth (1985), indicated that the abundance of blue-green algae was negatively correlated with high temperature; in contrast to laboratory studies that show that many species tolerate high temperatures. Chrysophytes (green algae) were the least affected by high temperatures in their study. Similar to vascular plant species, and probably for the same reasons, algae increase in number during certain seasons. Algal density showed peaks in late fall and late spring in Utah (Johansen and Rushforth 1985).

Cryptoendolithic algae live beneath sandstone and include species of cyanobacteria. Pale-colored sandstone formations have the most diverse and abundant communities (Bell and Sommerfeld 1994), In PJ woodlands, cryptoendolithic algae have been found under crusty sandstone-derived substrates (Ladyman, personal observation). These organisms may contribute to nitrogen cycling and weathering activities.

Lichens

Lichens are the product of a symbiotic partnership between fungi and algae. Fungal partners, usually the Ascomycete or Basidiomycete classes, provide structural support by enclosing the algae within the lichen body. They also supply the algae

with a relatively stable micro environment and nutrients from the substrate. Algal partners are frequently free living in the environment. The algae, the photobiont in this symbiotic relationship, provides carbohydrates from photosynthesis. Some photobionts (cyanobacteria) fix atmospheric nitrogen, which provides the fungus with a source of nitrogen in a nitrogen-deficient environment. Lichens grow on soil (terricolous lichens), on rocks (saxicolous lichens), bark (corticolous lichens), and wood (lignicolous lichens).

A typical lichen thallus is divided into three main layers; upper cortex, algal layer, and medulla. In some lichens there is a fourth, lower, cortex layer (Figure 1). The algal cells may form an almost continuous layer or occur in scattered clumps. The cortex is composed of compact fungal cells forming a protective covering. There are three morphologically recognizable types of lichens: foliose, crustose, and fruticose. Foliose lichens are generally leaf-like often with both an upper and lower cortex covering their outer surface. Crustose lichens have only an upper cortex. Fruticose lichens are radially symmetric and are enclosed by an outer cortex. The lower cortex, when present, often produces hairlike structures called rhizines that secure the lichen to a substrate. Exceptions that frequently occur in PJ woodland are *Peltigera*, a gray leaf-like foliose lichen without a lower cortex, and *Collema*, another foliose lichen, which is gelatinous when wet and lacks an upper cortex. The algae associated with the lichen *Collema* are cyanobacteria. Cyanobacteria give the lichen its black color and permit it to photosynthesize and fix nitrogen.

Lichens reproduce in several ways; the most simple is by asexual fragmentation. Stepping on a patch of lichen produces many fragments, each with the potential for starting a new colony. However, vigorous crushing, especially when dry, causes excessive fragmentation and leads to total lichen destruction (Pegau 1970; Harper and Marble 1988). Many lichens reproduce by producing small asexual structures that contain fungal and algal symbionts. A third method of reproduction is by spores. Depending upon the lichen species, spores occur in disc- or cup-shaped structures on the upper lichen surface, or on flask-shaped structures within the thallus of many crustose lichens. Several theories exist on the possible mechanisms of lichen sexual reproduction, but none have been demonstrated in nature. Algae reproduce mainly by mitotic cell division within the lichen thallus.

Lichens are remarkable because they can endure long periods (often several years) of desiccation and, after water absorption, regain full physiological function. However, photosynthesis occurs only when their thalli are moist. Although the water content of lichens is dependent on atmospheric conditions, they are capable of absorbing sufficient atmospheric moisture to photosynthesize even when the atmosphere is not fully saturated (Lange, Schultze, and Koch 1970). Crustose lichens are especially common in water-limited sites; whereas the foliose and fruticose lichens are more common in shady, relatively moist areas. Of the three morphological types, crustose lichens are less sensitive to air pollution and are in higher proportions in lichen communities in arid environments; this implies a greater tolerance to adverse conditions (Marsh and Nash 1979).

Commercially, lichens have been used to dye cloth in the Southwestern United States (e.g., *Xanthoparmelia chlorochroa*, a yellow-green foliose terricolous lichen, is used by Navajo Indians to weave in rugs and blankets) and in Lapland, Scotland, and other parts of Europe (Laudon 1986). The orchil lichen *Roccella* is used by chemists to make litmus; a substance that turns blue by alkalis and red by acids (Laudon 1986). In the Middle Ages, *Lobaria pulmonaria* was used to treat pulmonary disorder and *Parmelia sulcatus* was used for cranial disorders. Although these uses may seem
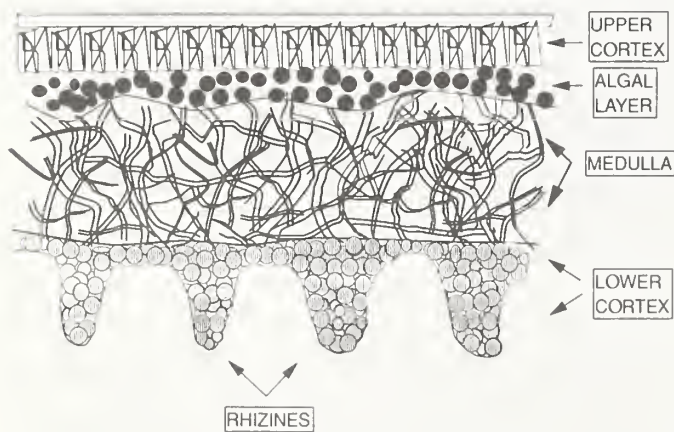

Figure 1. Cross section of a typical lichen thallus.

unfounded, many lichen acids do inhibit certain micro-organisms including bacteria. Usnic acid, produced by *Cladonia stellaris*, was a standard treatment for skin infections into the middle of this century. Lichen are used worldwide as a source of nutrition. *Umbilicaria* species are delicacies in Japan (Vitt et al. 1988). Reindeer moss is actually a lichen and is a major food for reindeer in Fennoscandia and caribou in Canada (Laudon 1986). Lichens have also been used to set the fragrance in French perfume, ferment beer, and make toothpaste. Two other unusual uses of lichens are as a wolf poison and a tobacco substitute. For more information on the structure and function of these organisms see Hale (1979) and Vitt et al. (1988).

Mosses and Liverworts

Mosses (Musci) and liverworts (Hepaticae) are known as bryophytes (Figure 2). In PJ woodlands, mosses often form a cushion at the base of trees, shrubs and in grass tussocks, and are usually easy to see. They range from one millimeter to a few centimeters tall; are green, drying to brown or black; mosses are sometimes a silvery white. Their ability to dehydrate and then rehydrate to be fully functional within a few minutes is important for survival in arid and freezing environments. A mature moss plant consists of a stem with leaves anchored to the substrate by rhizoids. A mature liverwort plant includes a stem with either leaves or a thallus, anchored to the substrate by rhizoids (Conard and Redfearn 1979).

Mosses and liverworts reproduce vegetatively (by fragmentation and regeneration), by propagula (a structure composed of multiple cells that becomes detached from the parent and develops into a new plant), and sexually by forming spores. Spores withstand adverse environmental conditions and only germinate on a suitable damp substrate. Upon germination, they usually develop a branched green structure that looks like a mat of algae-like filaments. Colorless rhizoids develop and penetrate the substrate, and finally small knots of chlorophyll bearing cells develop into leaves (or thalloid) and stems (Figure 2). More information is in Conard and Redfearn (1979).
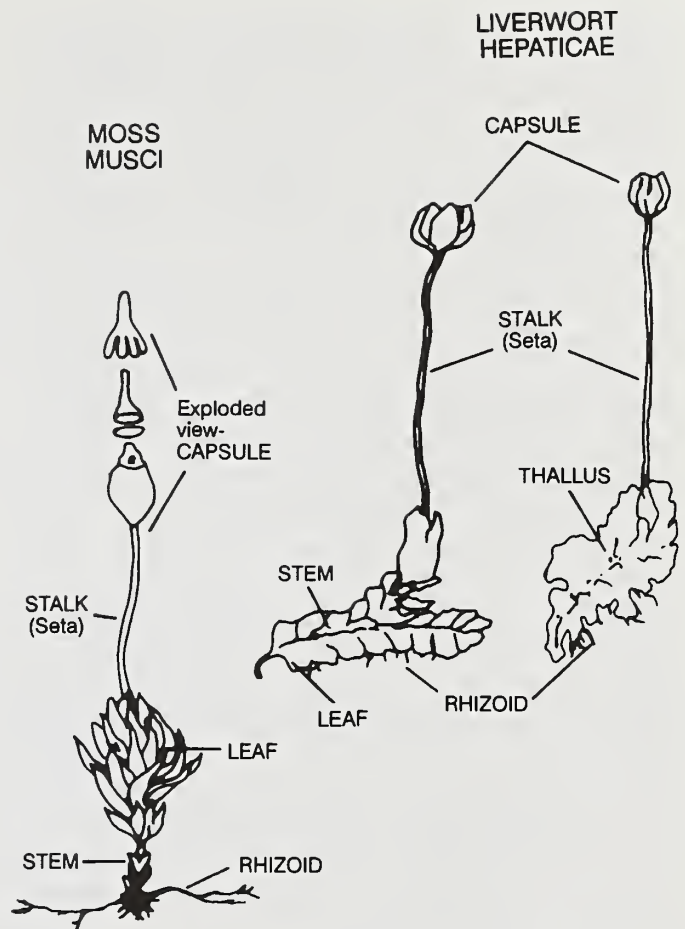
Figure 2. Schematic drawing of a moss and the two morphological types of liverwort.

COMMON SOUTHWESTERN CRYPTOGAM SPECIES

Studies that catalog cryptogams in the Southwestern United States include: Shields 1954; Prior 1969; Egan 1972; Flowers 1973; Anderson and Carmer 1974; Anderson and Rushforth 1977; Johansen and Rushforth 1985; Nebeker and St. Clair 1984; Ashley et al. 1985; St. Clair et al. 1993. In contrast to vascular plants, there is a great deal of lichen and algae species overlap in native cryptogam communities worldwide (Looman 1964; St. Clair et al. 1993). Algae have wide dispersal because their spores are wind borne (Schlichting 1969). In a study to define plant characters of the steppe and desert, the lichen *Diploshistes* is described as a distinctive indicator of steppe in Asia, in similar habitat in South Africa, and is equally common in Southwestern semi-desert regions

(Reichert 1936). *Dermatocarpon* species and *Psora decipens* are also common in these three geographically diverse regions. Lichens found in a study of cryptogamic crusts in the badlands of Spain were similar to those found in the Southwestern United States. The unspecified black crust that was described is probably composed of blue-green algae (Alexander and Calvo 1990).

The relative proportions of the life forms that compose cryptogamic crust differ throughout the world. In the Southwestern United States, lichen and blue-green algae are important components (Belnap 1993). Upland, sandy PJ woodland sites in the intermountain region are dominated by various lichen species of *Psora*, particularly *P. cerebriformis, P. tuckermanni* and *P. decipiens. Catapyrenium lachneum, Endocarpon pusillum, Xanthoparmelia chlorochroa*, and *Agrestia hispida* are also present in this area (St. Clair et al., 1993). Species of *Cladonia, Diploschistes,* and the vagrant *Xanthoparmelia chlorochroa*, are abundant in some of the PJ woodland in New Mexico (Ladyman et al. 1993). Table 1 lists some of common lichens in PJ woodlands. Definitive species identification of lichens usually requires chemical testing; however, the genera are easily identifiable by morphological traits (e.g., Hale 1979).

Terrestrial algae also occur in habitats other than microphytic crusts. *Microcoleus vaginatus, Schizothrix penicillata, Scytonema tenellum,* and *Nostoc commune,* found in the cryptogamic crusts of the Western United States, are also found in fresh water habitats (Campbell 1979). Other members of the crust community, such as *Microcoleus chthonoplastes, Calothrix pulvinata* and *Schizothrix subconstricta,* also exist in marine environments (Campbell 1979).

The algae *Microcoleus vaginatus* is widespread in Southwestern soils where it favors sandy, sandy-loam, and gypsiferous soils (Anderson and Rushforth 1977; Ashley et al. 1985). *M. vaginatus* assumes a variety of shapes including a spiraled single filament, a straight single filament, or bundles of filaments enclosed in a thin or a thick sheath. However, it is easy to recognize this algae under a microscope by the tangle of empty, transparent and black strands (Thanks to J. Belnap, National Park Service, Utah for pointing this out to the authors). In some regions relatively large areas are littered with the flattened blue-green algae, *Nostoc commune.* In dry times this algae is black, dry, and brittle and is sometimes mistaken for plant debris, but during wet periods it is gelatinous and often has a translucent yellow-black color.

Moss and liverwort species are less researched. Common moss species include those from the genera *Grimmia* and *Tortula* (Klopatek 1991; Ladyman et al. 1993). In PJ woodlands, liverworts are apparently only occasionally encountered and are not often studied. Species of the genera *Riccia* are found in PJ woodlands in New Mexico (Ladyman and Muldavin 1994a).

HABITAT

Precise descriptions of the habitat characteristics for cryptogamic crusts are unavailable. Studies comparing the cryptogamic abundance between sites, must consider man-made disturbances that may not be part of the experimental design. For example, in the Castle Cliffs area of southeast

Table 1. Some common lichens in PJ woodland.

Agrestia hispida (Mereschk) Hale and Culb	*Peltigera rufescens* (Weiss) Humb
Buellia elegans (Poelt)	*Psora cereformis* W. Weber
Catapyrenium lachneum [1] (Ach.)R. Sant.	*Psora crenata* (Taylor) Reinke
Cladonia chlorophaea (Flk.) Spreng.	*Psora decipiens* (Hedwig) Hoffm.
Collema tenax (Swartz) Ach.	*Psora globifera* (Ach.) Massal
Diploschistes actinostomus (Pers) Zalhlbr.	*Psora tuckermanii* R. Anderson ex Timdal
Diploschistes scruposus (Schreb.) Norm.	*Squamarina lentigera* (Weber) Poelt
Endocarpon pusillum Hedwig	*Toninia aromatica* (Turner ex Sm.) Massal
Heppia lutosa (Ach.) Nyl.	*Toninia caeruleonigricans* (Lightf.) Th. Fr.
Peltigera aphthosa (L.) Willd.	*Toninia candida* (G.Web.) TH. Fr.
Peltigera canina (L.) Willd.	*Xanthoparmelia chlorochroa* (Tuck.) Hale

[1] Particularly common synonym = *Dermatocarpon lachneum* (Ach.) A. L. Sm.

Utah, cryptogam cover was found on the ridge tops and upper slopes, and to a lesser extent on the lower slopes and flood plain (Brotherson and Masslich 1985). High water velocity in areas beneath midslope could account for the lack of cryptogam cover, although increased grazing pressure on the lower slopes may also cause cryptogam cover deficiency. Junipers (*Juniperus oesteosperma*) occurred less frequently on the floodplain than the ridges and none were on the slopes. This may indicate that there was a removal of junipers with associated soil disturbance that modified cryptogam development.

Aspect appears to affect the abundance of cryptogamic cover. Nash et al. (1977) in Arizona, and Alexander and Calvo (1990) in the Spanish badlands, observed significantly more cryptogam cover on north-facing slopes in semi-arid or arid environments. In the Central Namib coastal desert of Africa, crustose lichens were more abundant on northeast and eastern-facing slopes, but fruticose and foliose lichens were most abundant on south-western facing slopes, which were probably the most mesic (Schieferstein and Loris 1992). The extent to which slope defines suitable habitat range of cryptogamic cover is not conclusive.

Algae, lichen, and moss species diversity is related to soil pH and electrical conductivity (Ali and Sandhu 1972; Anderson et al. 1982b). Green algae favor acid soil and blue-green algae favor alkaline soils (Starks et al. 1981). In Washington state, where soils are acidic, algae are mostly green rather than blue-green (Johansen et al. 1993). Electrical conductivity, which is directly related to the cation concentration of the soil, is a measure of salinity. Generally there is a negative correlation between electrical conductivity and species diversity.

In some areas, vascular plants and cryptogams have complementary habitat requirements (Carleton 1990). For example, vascular plans respond negatively to high soil salinity and posi-tively to sandy soil, while cryptogam cover is often abundant in saline conditions and less plentiful in sandy ones (Anderson et al. 1982b; Rosentreter 1986). In California's Death Valley, blue-green algae grow on crusts of salt and in puddles where the salt concentration is 6 percent. Crust-forming fungal mycelia were found in Death Valley that tolerated 10-12 percent brine (Hunt and Durrell 1966). The abundance of other minerals such as magnesium, iron, copper, potassium, and calcium also affects algal species composition (Starks and Schubert 1982). For example, all forms of magne-sium were negatively correlated with algal abun-dance; iron was positively correlated to algal abundance. In the Southwestern United States, cryptogams frequent shrubs and areas vacated by dead shrubs (Ladyman, personal observation). However, in African deserts, cryptogams were not found where shrubs used to grow (Schieferstein and Loris 1992).

In the Southwest, cryptogamic crusts favor finer textured soils (Kleiner and Harper 1972) and those with a high amount of silt (Anderson et al. 1982a; Anderson et al. 1982b). In another study, heavier textured soil with considerable salinity supported the most developed crusts (Anderson et al 1982b). The presence of gravels or pebbles, approximately 1 to 2 cm in diameter, is positively correlated to well-developed cryptogamic cover on intervening soil spaces (Ladyman et al. 1994b; see Fig. 4, pg. 10).

TERRICOLOUS CRYPTOGAM ECOLOGICAL FUNCTION

Soil Stabilization

Background

Erosion causes an almost irreversible loss in productivity. Erosional processes may also lead to an impoverished soil seedbank (Francis 1994). How wind and water contribute to erosion in semi-arid environments, such as in the Southwest, depends on the land use, soil conditions, and topography (Dorst 1971; Thomas and Tsoar 1990). Geologic soil formation is estimated to be one inch per 300-1000 years (Dorst 1971). Soil reductions in excess of this figure have been measured in the PJ woodlands (e.g., Carrara and Carroll 1979; Lusby 1979a; Doughty 1987) and result in irreplaceable losses. Since the 1940s, rainfall-induced (noncryptogamic) soil crusts have been known to negatively affect infiltration and plant germina-tion, and contribute to soil loss (Fletcher and Martin 1948). In contrast, observations were made in the Southwest that crusts composed of algae and lichen had a beneficial function; they reduced erosion and added organic matter to the soil (Fletcher and Martin 1948).

Cyanobacteria have long been recognized as early colonizers and stabilizers of disturbed land. Treub (1888) wrote that gelatinous and hygroscopic cyanobacteria covered and stabilized the arid soil after the volcanic eruption at Krakatoa. Early colonization by cyanobacteria proceeding to rapid natural succession by mosses and green algae is described by work of Schwabe (1972) and Brock (1973) in their work on Surtsey Island, Iceland. During 1968 and 1969 the soil mats were of blue-greens. By 1972 these mats had been replaced by green algae and mosses. This could reflect an acidification of the soil surface. Fritsch (1907) also observed the soil stabilizing properties of cryptogams. Booth (1941) reported that on red Permian clays and shales in Oklahoma, *Microcoleus* was probably the most widespread and abundant algae, and seemed to be important in preventing soil erosion. Subsequent to these early reports there is a growing body of quantitative evidence that cryptogamic crusts are important in stabilizing soil against erosional forces, especially in arid and semi-arid environments that cannot support lush grass growth and are particularly susceptible to erosion (Loope and Gifford 1972; Brotherson and Rushforth 1983; Muncher et al. 1988; Campbell et al. 1989; Kinnell et al. 1990; Yair 1990).

Foster (1982), working in range management, reported: "The C (cover management) factor is often the most important factor of the Universal Soil Loss Equation. At a site, it is often the only factor that a range manager may easily change to control erosion." The most important factor influencing infiltration and sediment production in the PJ woodland covered watersheds of New Mexico was total ground cover (Wood et al. 1987). Lusby (1979b) studied runoff and sediment yield from areas converted from sagebrush to grass in four watersheds in Colorado. Using linear regression analysis he concluded that reducing bare ground by 38 percent can result in a decrease of 73 percent in sediment concentration (Lusby 1979b). In PJ woodlands, the extent of soil erosion varied considerably between seasons due to environmental conditions; it was highest at the end of the freeze-thaw period of late winter. (Wilcox 1994). Wilcox (1994), also found that, although the extent of erosion was not linearly related to percent cover, the plot with more than 60 percent bare ground had approximately 3.8 times the sediment runoff than the plots where cover was more than 50 percent.

Examination of exposed tree roots in PJ communities on the western side of the Colorado Rockies, indicate that the erosion rate on northern slopes is about half that on southern slopes; the abundance of cryptogamic crusts on northern slopes could contribute to this difference (Carrara and Carroll 1979). This study also showed that the erosion rate on the southern slopes has almost quadrupled over the last century as compared to the preceding four centuries. The rates determined by Carrara and Carroll are described in Table 2. Continuing at the current rate, a 50 cm soil depth would be essentially eliminated in 279 years. The dramatic increase in erosion rate coincides with the introduction of intensive grazing, which would have severely depleted the cryptogamic cover. This rate of erosion agrees with sediment production data collected by Lusby (1979a) also from the Badger Wash drainage basin in Colorado. Under winter-long grazing pressure, sediment yield was 3.21 acre-feet/square mile/year (Lusby 1979a). This corresponds to 0.06 inches over the region. These results lead to an estimation that a soil depth of 50 cm, or 19.7 inches, would be essentially eliminated in 327 years.

Table 2. Rates of erosion in PJ communities on the western side of the Colorado Rockies (Carrara and Carroll 1979). Values were determined by examining exposed tree roots.

Period (years ago)	0-99	100-199	200-299	300-399
Erosion rate (mm/yr)	1.79	0.49	0.33	0.22

General cryptogam effects

The presence of an organic crust on the soil surface shields it from erosion (Harper and Marble 1988; Lancaster and Nickling 1994). Cryptogamic crusts stabilize soil by providing soil structure and promoting soil aggregation, although the mechanisms employed may be different among the different types of cryptogam. Moss rhizoids entwine through soil and hold particles in a fine mesh network, cyanobacteria filaments adhere to soil, and lichen-covered soil has a tangle of fungal hyphae (fine threadlike structures that are attached

to the thallus) that both weave the soil particles together and adhere to them (Schulten 1985). Finer particles, such as silt and clay, are found on bare soil surfaces, whereas cryptogamic-covered soil has a much higher proportion of larger particles (Fletcher and Martin 1948; Eldridge and Green 1994). Schulten (1985) quantified these observations in southeast Iowa in soils that were primarily composed of fine to coarse sands and gravel. The study looked at soil particle (aggregate) size beneath cyanobacteria-covered, lichen-covered, moss-covered, and bare soils. Aggregate particles greater than 2000 µm in size were more abundant under the cryptogam covered soil, particularly that dominated by cyanobacteria, than under bare soil. Under bare soil the particle-aggregate size was typically 500-250 µm. The soil surface silt fraction, studied in four watersheds in New Mexico, was the second-most important variable influencing sediment production (Wood et al. 1987). These results indicate that increases in the coarseness of surface aggregates will reduce sediment production.

Nutrient status is also related to soil texture. Nitrogen is a major nutrient lost from eroded sediments (Burwell et al. 1975). Finer soil particles with their relatively large surface area and higher exchange capacity, adsorb a greater amount of nutrients such as nitrogen than coarser particles (Pallis et al. 1990). Fine particles tend to be most easily lost by wind and rain. Therefore, there is a proportionally higher loss of nitrogen and minerals, and ultimately productivity, from lost fine soil particles than from coarser particles. Therefore, it is likely that the nutrient loss is proportionally less from cryptogam-covered soil than from bare soil because there is less loss from the finer fraction.

An additional benefit of the organic crust derived from the algae, *Microcoleus vaginatus*, is that, even with no living cells, the old sheaths persist as a dense mat on the soil surface and protect it against erosion (Durrell and Shields 1961; Anderson and Rushforth 1977; Belnap and Gardner 1993). This network of filamentous cyanobacteria has been reported to be one to three inches deep in Colorado and Utah (Campbell 1979). *Microcoleus vaginatus* sheaths have been found up to 10 cm below the crust surface on undisturbed, sandy soils on the Colorado Plateau, indicating a significant contribution to soil organic content. Heavily trampled sites support only a thin veneer of algal cover (Belnap and Gardner 1993).

Algae and lichen also use another mechanism to protect the soil surface. They secrete mucilaginous polysaccharides that soil bind particles together into hydrophilic aggregates (Fletcher and Martin 1948; Lewin 1977; Belnap 1992; Starks et al 1981; Eldridge and Greene 1994). This property may promote water retention in the soil. Moss can also retain proportionally high amounts of water. A square yard of moss, weighing 2.2 pounds normally, retains 11 pounds of water after a heavy rain (Furon in Dorst 1971). Although the concept must be rigorously tested, the high water holding capacity of some cryptogamic cover may be likened to a sponge that reduces runoff during heavy downpours.

Wind erosion

To study the effects of wind on soil loss from cryptogam-covered surfaces, Williams et al. (1993) set up an open-bottomed, portable wind tunnel in areas between shrubs at Capitol Reef National Park, Utah. Experimental plots were classified as having; "extensive microphytic crust development," "crust removed with a small blade," and "crust chemically killed." The threshold velocity needed for soil particle movement was highest on undisturbed plots. Lancaster and Nickling (1994) found that even weak cryptogamic crusts significantly increased the threshold wind velocity leading to wind erosion; crust disturbance reduces the threshold velocity. MacKenzie and Pearson (1979) reported that sand covered by the green alga, *Microspora*, withstood twice the wind velocity as bare sand before significant erosion occurred.

Water erosion

Depending upon the species composition cryptogamic crusts can either increase or decrease water infiltration (Graetz and Tongway 1986; Harper and Marble 1988). Moss and some lichen-dominated crusts increase permeability (Johansen 1986; Brotherson and Rushforth 1983); some algal dominated crusts reduce permeability (Fletcher and Martin 1948; Johansen 1986; Eldridge 1993a; Eldridge 1993b; Brotherson and Rushforth 1983). A

study in PJ woodland in northern New Mexico examined infiltration by recording the difference in pH at levels immediately below the crust and at a depth of 10 cm (Ladyman et al. 1993). The speculative theory is that leaching is indicated if the pH immediately under the soil surface is less than that at a depth of 10 cm. The results of these preliminary studies support the theory that moss-dominated crusts enhance infiltration and blue-green algae-dominated crusts retard infiltration. The effect of cryptogams on soil pH *in situ* requires investigation.

Lessening runoff by increasing infiltration is a straightforward concept. However, Booth (1941) reported that even where algal mats retarded infiltration, soil losses were still far less than from bare soil plots, and that there was "little or no cutting, nor was the runoff water muddy." Recent reports confirm that infiltration is reduced while overall sediment loss is also reduced (Loope and Gifford 1972; Eldridge and Green 1994). This may be because the cryptogamic cover binds soil aggregates and reduces sediment losses although the water run-off amount is greater than on disturbed surfaces.

Figure 3. A view of an area subject to grazing in southeastern Utah. *Artemisia tridentata* is in the foreground and pinyon-juniper woodland in the distance. Note the cryptogamic cover is under the shrubs.

This is not, however, the situation in all instances (Harper and Marble 1988). In PJ woodland of southeast Utah, where lichen-covered soil had reduced intrinsic permeability, the cryptogam-covered soil demonstrated greater overall infiltration and lower sediment production than areas that had been chained four years earlier and had bare soil (Loope and Gifford 1972). Another study in PJ woodland of northeast Arizona (Beymer and Klopatek 1992) where cryptogam-covered areas were compared to areas that had been disturbed (resulting in loss of cryptogam cover), supports the

Figure 4A. The cryptogamic crust is composed of blue-greens and lichens, including species of *Cladonia*. A. The grasses are growing completely surrounded by the lichen cover in some areas.

Figure 4B. In other areas, especially in the shade of tree canopy, grasses are sparse and *Peltigera* species (white lichen in photo) are present. Small gravels (1-2 cm) are correlated with abundant and well-developed cryptogam cover (Ladyman et al. 1994).

Figure 5. A hummocked cryptogam (lichen, moss, and algae) covered soil in pinyon-juniper woodland in Southwest Colorado.

observations of Loope and Gifford (1972). An explanation for this apparent anomaly is that cryptogams increase rugosity (a term used to describe wrinkling, corrugation or roughness) of the soil surface (West 1990). Therefore, even though the mucilaginous secretion from a dense algal or fungal mat may reduce infiltration, the complex micro-topography of the soil surface slows runoff by making the water puddle (See Figures 3-7). Water then gradually infiltrates the soil and sheet erosion is avoided (Brotherson and Rushforth 1983b; Eldridge and Greene 1994).

The apparent contradiction of increased water infiltration with reduced permeability of the soil surface can be explained in physical terms. A very thin film of water at the soil surface increases raindrop detachment (Ferriera and Singer 1985) although slightly deeper films (puddles) can lead to reductions in detachment (Moss and Green 1983). Therefore, reduced sediment in the presence of the pedicelled and roughed cryptogamic surface may result from the localized retention of a sufficiently deep film of water (i.e., puddles). In addition, the uneven soil surface may effect capillary forces between soil surface and individual soil particles and provide enhanced interception niches for splashed material (Eldridge and Green 1994). A high degree of rugosity is also likely to increase the surface area available for infiltration. Therefore, the cryptogamic crusts meet a defined criteria for reducing soil erodibility from water by resisting splashing and water abrasion (Foth 1978). They may not stop water dispersion over short distances but they act to reduce long distance transporting forces that set up rills and contribute to sheet erosion.

As in the arid regions described by Johansen (1986), cryptogamic crusts in PJ woodland have two types of morphology: relatively flat with a considerable number of cracks, or hummocked with a complex of pinnacles and pedicels (compare Figures 6 and 7). Insufficient studies have been

Figure 6. A light covering of predominantly blue-green cryptogamic cover. The pedicel and hummocked characteristics have not yet formed and this cover is judged to be early in its development.

Figure 7. There is still some bare ground but the pedicelled cryptogamic crusts are thicker among the grass.

conducted but it is probable that the flatter surfaces are experiencing early recolonization after disturbance and the hummocked surfaces are mature and older (e.g., Johansen and Rushforth 1985). The flat crusts may not be able to slow runoff to the extent that a more mature, hummoked crust can, so until a complex micro-topography develops, the soil stabilization and sediment reduction benefits may not be evident. A measure of surface roughness that includes the degree of cryptogam cover is important when determining the potential soil loss from sagebrush (Johnson and Blackburn 1987). In this study surface roughness was positively correlated to low surface runoff.

The effect of cryptogam cover on reducing sediment depends on soil type. In a study done near Tucson, the runoff from a newly-bare un-stable alluvium soil was about double that from an equivalent algal-encrusted surface; the runoff from a granitic upland soil where the cryptogam layer had been removed by scalping was about the same as that with the cryptogam layer in place (Fletcher 1960). A problem with using scalped plots to simulate bare ground (Greene et al. 1990; Graetz and Tongway 1986) is that the newly scraped surface will have different infiltration characteristics than a surface exposed to rain, wind, and compaction forces (Eldridge 1993b). However, scalped plots were found to have comparable properties to overgrazed surfaces in the Australian desert (Graetz and Tongway 1986)

Unfortunately, much of the older sediment loss/infiltration research omits cryptogam cover and only describes vascular plant cover. For example, information can only be inferred from a study in PJ (*Pinus monophylla* and *Juniperus osteosperma*) in Nevada (Blackburn 1975). The soil surface was described as having a fairly level relief but surface roughness showed a positive correlation with increased infiltration. The conclusion of the investigator was that there was an indication that an irregular surface may increase infiltration rates. Surface roughness (and the photographs) suggest that cryptogamic cover was present but cryptogams *per se* were not considered at the time.

In a nutrient-deficient environment, consideration of infiltration measurements alone may miss other ecological consequences of water movement into and through the soil. Low cation exchange capacity is associated with disturbance (Graetz and Tongway 1986). Rapid infiltration rates and low cation exchange capacity in the topsoil reduces the soil nutrient content as top soil nutrients are washed down through the soil and away from the plant root zones (Graetz and Tongway 1986). This suggests that slower infiltration rates due to cryptogamic cover will reduce nutrient loss. Deeper water penetration under cryptogam-covered areas has been observed (Brotherson and Rushforth 1983). Possibly, this would benefit shrubs and may indicate that water storage is increased.

Cryptogam soil stabilization outside the United States

Increased effective infiltration and reduced erosion rates despite reduced permeability (Johansen 1986) is not restricted to the Southwest. In the badlands of Spain, there was lower sediment concentration (3-5.2g/l) from cryptogam-covered areas than from areas without lichens (average sediment concentration 20.3g/l; Alexander and Calvo 1990). These authors found that the decrease in sediment wash occurred in spite of rapid ponding and potential runoff generation. They observed that the rough, uneven pedicels on the soil surface allowed the water surplus to be locally redistributed and eventually infiltrate.

Information on the influence of cryptogamic cover on sediment loss and infiltration is available from arid and semi-arid parts of Australia, which have also experienced overgrazing (Francis 1994). These lands support shrubs such as *Atriplex* species (saltbush), eucalyptus woodlands, and grasslands. The structure of cryptogam and associated vascular plant cover varies considerably throughout continents and cannot automatically be compared. Unlike the cryptogam cover in parts of the Asian[1] desert and steppes, which is associated with a dense *Carex* cover (Pabot 1980) and is not observed in the PJ woodlands of the Southwestern United States, the cryptogam and vascular plant cover in Australia appears to be quite similar to

[1] *Asia includes: the Middle East (Palestine to the Syro-Turkish border and from the Persian Gulf up to the Iranian and Afghan borders with former Soviet Republic), North Africa, Siberia, North India and possibly into Tibet and Mongolia (Pabot 1980)*

that in parts of the Western United States. This fact, along with a similar soil type (aridisols) (Buckman and Brady 1969), suggest that the research observations from Australia may be relevant to lower elevation PJ communities in the United States. Several of the same problems associated with land use must be confronted on both continents.

In Australia, cryptogamic covered soil was significantly less susceptible to splash erosion (Eldridge 1993a). Crusts with progressively decreasing cryptogam components exhibited increasing proportions of sheet-like and sealing components that reduced infiltration and increased erosion (Muncher et al. 1988). In Australian *Atriplex* shrub land, evidence indicates that precipitates form at a shallower depth beneath overgrazed surfaces as compared to cryptogam-covered surfaces (Graetz and Tongway, 1986). When fire destroyed the cryptogams, rain-impacted shallow flows initiated rills and significant soil surface degradation occurred (Kinnell, Chartres, and Watson 1990). More sediment was lost under simulated rain showers from plots of bare ground and with low cryptogamic cover than from plots covered by more cryptogam cover (Eldridge and Greene 1994). As well as differences in the amount of eroded material, there were differences in particle (aggregate) size between plots of different coverage; more fine-sized (silt and clay) particles were lost from bare and low-coverage plots compared to losses from cryptogam and vascular plant covered plots. Eldridge and Greene (1994) attributed this to the aggregating properties of the cryptogams.

Nutrient Cycling

Nitrogen fixation

Cyanobacteria and lichens containing cyanobacterial symbionts are capable of nitrogen fixation. Cyanobacteria are routinely and effectively used in agriculture as *in vivo* producers of crop-available nitrogen (e.g., Isichei 1990; Dadhich et al. 1969).

The method used to measure nitrogen fixation influences the results. The most common method, using a gas chromatograph, measures ethylene reduced from acetylene by the nitrogenase enzyme (e.g., Nakatsubo and Ohtani 1991). Although this method can be reliable, results should be carefully interpreted. Often three is used as the conversion factor between the number of acetylene molecules reduced per molecule of nitrogen fixed, but for precise estimation the number should be determined using nitrogen-15 (^{15}N) (Weaver 1986). Other considerations particularly relevant to nitrogen measurements in cryptogams have been reported. Extended exposure to acetylene results in abnormally high rates of acetylene reduction in *Peltigera polydactyla* (MacFarlane et al. 1976) and *Anabaena* species (Nielson et al. 1971), thus overestimating the nitrogen fixation rate. Also, consider the extent of crust hydration when using short-term results and extrapolating them to longer terms. For example, following rehydration nitrogen fixation increases at different rates depending on the species; therefore, the levels measured at different times either remain constant or drop off (Kershaw 1985).

In studies of nitrogen fixation and photosynthesis, the thallus and air temperature can differ. This was not considered in many early field studies. Cryptogamic crust microclimate can significantly vary from the environment. For example, the temperature and humidity profile was significantly different at 0, 3.75, and 8.75 cm above the soil surface through a thick mat of *Cladonia alpestris* (Kershaw and Field 1975). Also, the experimental environment of a measuring chamber often imposes changes. Although adequate field instrumentation and experimental design are required to meaningfully interpret results, the recent availability of microelectronic thermometers, thermistors (to measure humidity), light sensors, and sophisticated measuring chambers, helps to ensure more accurate data collection and conclusive results from nitrogenase field studies.

A more recent approach to studying nitrogen fixation utilizes stable isotopes (Griffiths 1991). This method has been used in determining the contribution cryptogams make to the nitrogen balance in an ecosystem (Evans and Ehleringer 1993). This method is based on measuring the relative abundance of the two stable isotopes of nitrogen, nitrogen-14 (^{14}N) and ^{15}N. On average ^{14}N comprises 99.63 percent and ^{15}N only is 0.37 percent of total nitrogen in the atmosphere. A differential notation ($\delta^{15}N$) is used in all stable isotope

studies and relates the sample amount of the different isotopes to a standard and is expressed as parts per thousand ($^\circ/_{\circ\circ}$).

The nitrogenase enzyme differentiates between ^{14}N and ^{15}N. Due to this property of the nitrogenase enzyme, the proportion of ^{15}N in tissues of nitrogen-fixing organisms is less than in tissues of non-fixing organisms. In non-fixing organisms the nitrogen source is from soil. Soil nitrogen tends to be enriched with ^{15}N. The proportion of ^{15}N in the soil is, on average, $\delta^{15}N = 9.2 ^\circ/_{\circ\circ}$ (Ehleringer and Osmond 1989). The value for tissue of a nitrogen-fixing organism that obtains all its nitrogen from the atmosphere, via the nitrogenase enzyme, is $\delta^{15}N = 0 ^\circ/_{\circ\circ}$. Using a mass spectrometer, samples of soil, vascular plants, and cryptogams, can be analyzed for the abundance of the two isotopes and the proportion of nitrogen from directly fixed nitrogen can be determined (For more information see reviews by Griffiths 1991 and Ehleringer and Osmond 1989).

Seasonal cryptogam productivity is estimated by studying the effect of individual environmental parameters on nitrogen fixation and photosynthesis. Air temperature affects nitrogenase activity in a species-specific manner. The temperature for optimal activity in lichens is between 20 to 30°C (Kershaw 1985), but ranges from 15°C in *Solorina crocea* and *Nephroma arcticum* (Kallio et al. 1972 in Kershaw 1985), to 16-21°C in *Peltigera canina* (Maikawa and Kershaw 1975), to 35°C in *Peltigera rufescens* (Hitch and Stewart 1973). However, at high temperatures the lichens and algae tend to rapidly dry out, so a higher level of nitrogen fixation does not mean greater long-term production. A complete absence of nitrogenase activity has been reported under snow cover (Kershaw 1985). But Kershaw and MacFarlane (1982) have measured nitrogenase activity of *Collema furfuraceum* at thallus temperatures as low as -40°C. Snow cover apparently causes depletion in carbohydrate reserves and the low-light environment prevents adequate photosynthesis to support of nitrogen-fixation. Early studies concluded that no nitrogen fixation occurs in the dark (Kallio et al. 1972 in Kershaw 1985), but Hitch and Stewart (1973) later determined that if more realistic dark periods (i.e., like those encountered in nature) were used, nitrogen fixation does occur. Field studies in creosote bush communities in New

Mexico confirmed that lichen and algal nitrogen fixation occurs in light and dark conditions (Johnson 1982). However, because nitrogen-fixation during dark periods relies on stored carbohydrate resources, day/night length and conditions for photosynthesis in the preceding light period are determining factors.

Nitrogenase activity in cyanobacteria is limited by water availability (Nakatsubo and Ino 1987). Nitrogen fixation increases as soil moisture increases (Terry and Burns 1987). In PJ woodlands, cryptogams exhibited higher rates of photosynthesis and nitrogen fixation in early spring when there was moisture from snow melt, than in late summer when there was only moisture from convectional precipitation (Klopatek and Thomas 1994).

Disturbance of cryptogamic crust significantly reduces the amount of nitrogen fixed (Terry and Burns 1987; Belnap et al. 1994; Evans 1994). A dramatic drop in nitrogenase activity was observed after a single footprint disrupted the cryptogamic crust in an undisturbed grassland in Utah (Belnap, National Park Service, Utah, personal communication with Ladyman).

Mayland and McIntosh (1966) used chambers enriched in ^{15}N and determined that native algal crusts actively fixed atmospheric nitrogen and that grass seedlings germinated and grown in the algal mat also contained products from atmospheric nitrogen. Whether the algae excreted nitrogenous compounds or whether the fixed nitrogen was available to the plants after algal death and decomposition, was not determined. Field studies showed that vascular plants, including grasses, growing with a cryptogamic crust contained more nitrogen than plants growing where the crust had been removed by trampling (Belnap 1992).

Leaf litter may also affect the amount of nitrogen fixed by cryptogams. The leaf litter of shrubs such as *Atriplex*, *Artemisia tridentate* and *Ceratoides lanata* (winterfat) inhibits nitrogen fixation and nitrification (the oxidation of ammonium salts to nitrites and then nitrates) from 41 to 100 percent (West and Skujins 1977; Klubeck and Skujins 1980). Also, various forms of mineral nitrogen (e.g., ammonia) suppress nitrogen fixation in cryptogamic crust (Delwiche and Wijler 1956; Reddy and Giddens 1975; Klubeck and Skujins 1980). This occurs probably through a type of feedback inhibition of the nitrogenase enzyme.

Cryptogamic crusts provide the major portion of nitrogen in desert and semi-desert ecosystems (Rychert and Skujins 1974; West and Skujins 1977; Evans and Ehleringer 1993; Evans 1994). Nitrogen fixation rates range from 10 to 100 kg nitrogen/ha/yr (West and Skujins 1977; Harper and Marble 1988) in some systems, to 2 to 41 kg nitrogen/ha/yr (West 1990) in others. In PJ woodlands in northern New Mexico, reported nitrogen fixation rates were 12.6 to 14.3 kg nitrogen/ha/yr (Loftin and White 1995). The range of nitrogen fixation is probably a consequence of diurnal, environmental, and seasonal variability. Vascular plants use approximately 10 to 12 kg nitrogen/ha/yr in Utah deserts (Harper and Marble 1988). Estimates are that more than 70 percent of nitrogen fixed is lost through denitrification (reduction of nitrates or nitrites) by soil micro-organisms and evaporation (West and Skujins 1977). Input by atmospheric nitrogen deposition is less than 4 kg nitrogen/ha/yr (Evans and Ehleringer 1993). There are few sources of fixed nitrogen, besides cryptogams, in these ecosystems to supply the needs of vascular plants. (West and Skujins 1977; Harper and Marble 1988).

Biomass/organic matter

The three ways cryptogams add organic matter to their environment are through:

1. Loss of carbon and nitrogenous compounds after membrane destruction in wetting/drying cycles (Tearle 1987);

2. Active secretion of carbon and nitrogenous compounds into the soil; and

3. Accumulation of biomass following death.

Release of polysaccharides by algae is well documented (Lewin 1977). Beymer and Klopatek (1991) studied radioactive carbon (^{14}C) accumulation under algal-lichen crusts in PJ woodland in northern Arizona. Their data show that microphytic crusts may contribute from 43 (in grazed areas) to 350 (in ungrazed areas) kg carbon/ha/year in these woodlands. Also, as much as 2.5 kg carbon/ha/year may be directly secreted into the soil (Beymer and Klopatek 1991). Thus, cryptogams can make a significant contribution to soil building in these environments. Nutrients are probably leached into the soil and may contribute

to the nutrition of soil micro-organisms (Harper and Pendleton 1993). In their comparison of pristine and grazed areas in southern Utah, Kleiner and Harper (1972) noted that there was less soil organic matter at grazed sites where the cryptogamic cover was absent. Soil organic content was higher in *Collema*-cyanobacteria crust than in adjacent bare soil (Kleiner and Harper 1977b; Harper and Pendleton 1993).

The amount of soil organic matter contributed by cryptogamic crusts may depend on its micro topographical relief. Tall pinnacled (pedicelled) crusts have higher carboxylation rates (a measure of photosynthetic activity) and greater dark respiration than low pinnacled crusts (Jeffries et al. 1989). This may be because of crust maturity and/or number of organisms present. Cryptogamic crusts in black brush communities in southern Utah had net photosynthetic activity above maintenance levels in the wet spring. Therefore, the potential for biomass production existed during this season (Jeffries et al. 1993a). Because these crusts had high resaturation respiration, slow net photosynthetic recovery after rehydration, and negative net photosynthesis at relatively high water contents, they are probably not particularly well adapted for producing biomass in the very-wet/very-dry cycles that occur in summers in the Southwestern United States (Jeffries et al. 1993b).

CRYPTOGAM COVER AND VASCULAR PLANTS AND FAUNA

Vascular Plant Nutrient Status

Cryptogamic cover significantly alters the nutrient availability to higher plants. Phosphorus, potassium, calcium, magnesium, and iron are often taken up by higher plants in larger quantities when cryptogamic cover is present (Belnap 1992; Harper and Pendleton 1993); although, sometimes cyanobacteria compete for phosphorus and iron (Harper and Pendleton 1993). Small annual plants and perennial seedlings that have a large portion of their roots in the upper soil levels benefit the most from cryptogamic crust (Harper and Van Buren 1994). Additionally, annual plants are often larger and more abundant seed producers if intermixed with cryptogamic cover (Belnap in Harper and Pendleton 1993; Harper and Van Buren 1994).

Compared to plants growing in the absence of cryptogams, *Festuca octoflora* and *Mentzelia multiflora* had significantly higher amounts of nitrogen, magnesium, and iron (Harper and Pendleton 1993). *Festuca* also had a higher percentage of phosphorus, potassium, and calcium while *Mentzelia* had a higher percentage of sodium. The weight and tissue content of potassium, sodium, and copper in *Lepidium montanum* was significantly reduced when the crypto-gamic crust was removed by scalping two months before measurement (Marble in Harper and Pendleton 1993).

An explanation for these observations could be that minerals are more available to higher plants in the presence of a cryptogamic cover. One mechanism for this could be because clay particles in conjunction with lichen and algae polysaccharides form relatively large surfaces of negatively charged ions that strongly bind to more positively charged ions (Lewin 1977; Belnap and Gardner 1993). These bound minerals then remain exchangeable at the soil surface rather than leaching away by water percolation or becoming bound in a chemically unavailable form (Belnap and Gardner 1993). Another possible mechanism is the potential production of chelating agents called phytosiderophores (Takagi et al. 1984; Mino et al. 1981). Phytosiderophores are partially or wholly specific to chelating (binding) individual minerals, and increase the accessibility of those minerals to vascular plants. Secretion of ion binding substances has been observed for algae (Lewin 1977; Barclay and Lewin 1985; Harper and Pendleton 1993). Therefore, higher levels of minerals in vascular plants associated with cryptogams may be because of organic chelating agents secreted by the cryptogams. However, the effect of cryptogamic secretions on soil pH and nutrient availability requires further investigation.

In the Negev Desert in Israel, Zaady and Shachek (1994) tested the hypothesis that patches of microphytic soil crust act as sources of water and nutrients, while macrophytes (shrubs, annuals, herbaceous perennials) act as sinks for the water and nutrients. They manipulated patches by herbicide spraying, scraping, and grazing. Their results supported their original hypothesis that patches of vascular plants act as sinks. The patch-like structure of the Southwestern landscape appears to be natural (O'Neil et al. 1991) and such a source/sink relationship within communities should be investigated more fully.

Interactions with Vascular Plants

Conservation of terricolous cryptogam species may help maintain the biodiversity of other plant species. Spatial coverage by cryptogamic crusts has been positively correlated with plant diversity (Harper and Marble 1988; Beymer and Klopatek 1992). Although research on the interactions between cryptogams and higher plants is not extensive, there are two examples in the Western United States. The regional endemic *Arabis fecunda* occurs in montane-juniper woodland, ponderosa pine, and *Agropyron-Festuca* grasslands. In areas not subject to trampling, *Arabis fecunda* was more abundant on cryptogam-covered areas (Lesica and Shelly 1992). In studies to determine the habitat requirements of the rare dwarf bear-claw poppy (*Arctomecon humilis*) at least 84 percent of the total living cover on poppy-supported sites was a soil-surface cryptogam community (Nelson and Harper 1991).

Vegetation cover composition is closely associated with soil features (e.g., depth, pH, mineral content) and climatic conditions. Rosentreter (1986) showed that a mosaic of subtle differences in soil characteristics influence community pattern in Idaho. In his study region the areas dominated by lichen soil crusts were more salty than areas where *Chrysothamnus naseosus-Poa*-moss communities were found. He determined that the lichen soil crusts were a climax soil group existing after the rabbit brush-*Poa*-moss community composition changed to *Artemisia tridentate/Agropyron spicatum* habitat type. His studies on post-fire species composition indicated that the lichen soil crust on very thin soil acted as a refuge from fire for species in the adjacent deeper, less salty soils. The lichen dominated patches appeared to influence the post-fire composition of the entire study area.

The interaction between vascular plants and cryptogams has been described as a one-to-one tradeoff (West 1990); implying that cryptogamic cover and grass cover are mutually exclusive. However, the association between cryptogamic cover and vascular plants is complex. For example, cryptogamic crusts that raise soil temperatures because they are darker than bare soil, could increase seedling germination in the spring (Harper and Pendleton 1993). Some seedlings would be favored over others; therefore, there

maybe a physiological association between vascular plants and cryptogams that is not a competitive or allelopathic (growth suppression caused by toxic substance release) interaction.

Environments influence cover, but cover influences environments. For instance, extensive destruction of cryptogamic cover can lead to an increase in the albedo (reflective power) of the soil surface which may cause a relatively large-scale environmental change. Increases in the soil albedo cause local heat loss and change in air circulation (Francis 1994). A study on galleta- (*Hilaria jamesii*) and needlegrass- (*Stipa*) dominated sites, found that the galleta-dominated soil had a finer texture, higher surface potassium content, higher organic matter content, and a slightly but significantly, warmer average temperature than the needlegrass-dominated soil (Kleiner and Harper 1977a). Some of these differences may be because of cryptogamic cover rather than the cause of the community difference. Therefore, the reasons that lead to the structure of a community must be sought from a complex array of parameters.

Numerous studies indicate that cryptogams are not out-competing grass cover (Kleiner and Harper 1972; Kleiner and Harper 1977a; Anderson et al. 1982a; Anderson et al. 1982b; Jeffries and Klopatek 1987; Beymer and Klopatek 1992). An example is from a study of two areas in Utah that had similar soil and vegetation (Kleiner and Harper 1972). One site was a pristine area inaccessible to cattle and horses, and the other was an area with a history of light grazing. The area the vascular plants covered was similar at both sites and was probably limited by moisture. However, the cryptogamic cover was 33 percent higher at the pristine area (38 percent

cover at the pristine area versus 5 percent at the lightly grazed area). The cryptogam cover was an extra feature of the less disturbed community. Apparently, the moisture not used by the cryptogams was lost and vascular plants were not able to use it to cover more area.

In another study, a comparison was made between two grass communities (Kleiner and Harper 1977a). Cryptogam cover was similar on galleta grass-dominated sites and needlegrass-dominated sites (42 percent versus 37.9 percent). However, the vascular cover was 37.5 percent on the galleta-dominated area and only 19.3 percent on the needlegrass-dominated area. Evidently, the extent of grass cover was independent of the cryptogam cover. Jeffries and Klopatek (1987) studied four black brush communities in the Kaiparowits Basin of southern Utah and northern Arizona. These communities were classified as: relic (undisturbed); 10 years since heavy grazing; 3 years of light to moderate winter grazing; and approximately 100 years of heavy year-long grazing (Table 3). Under light to moderate winter grazing the grasses did not benefit from the cryptogam cover reduction; instead the grasses that tolerated grazing just filled in the spaces left by grazing intolerant grass.

In contradiction of opinions that cryptogams inhibit grass establishment (e.g., Savory 1988), studies on the vegetation cover of three undisturbed PJ communities on mesa tops in New Mexico (Ladyman and Muldavin 1994a) demonstrated that high grass cover and high cryptogam cover can coexist. In fact, the mesa with the highest cryptogam cover also had the highest grass cover (Ladyman et al. 1994b). Elevation, precipitation,

Table 3. Vegetative cover in four blackbrush communities with different grazing pressures. Soils were 87-99% sand and gravel, with a mean pH of 8.2 - 8.5 (derived from Jeffries and Klopatek 1987).

Cover	Relic (undisturbed) m²/ha	10 yrs since heavy grazing m²/ha	3 yrs light winter grazing m²/ha	100 yrs heavy grazing m²/ha
Total herbaceous	1047	127	256	102
Total cryptogam	2129	50	1196	70
Oryzopsis hymenoides	80	4	22	3
Hilaria jamesii	2	76	11	32
Total cover	6871	1549	4326	1576

and soil features all contributed to vegetation cover variation between mesa tops (Ladyman et al. 1993). The results indicated that there were positive and negative associations between individual plant species (Ladyman and Muldavin 1994a). For example, grama grass (*Bouteloua gracilis*), a major grass of the PJ woodland in New Mexico, southwestern Colorado, southeastern Utah, and most of Arizona, was significantly and positively associated with abundant cryptogamic cover. Needlegrass was, as in the study by Kleiner and Harper (1977a), negatively associated with cryptogamic cover.

It is likely that there are associations between specific species of vascular plants and specific species of cryptogams (Oksanen 1984). These associations arise from shared habitat requirements and/or specific growth regulator interactions. In addition to growth regulators, compounds such as vitamins and enzymes are also secreted by cryptogams (Harper and Pendleton 1993; Ladyman, unpublished data). There are environments appropriate for certain cryptogam species, while others exist for certain grass species, and still other environments are suitable for both. Thus, always consider perceived water and nutrient competition in conjunction with other environmental and soil conditions. Kleiner and Harper (1977a) demonstrated that frequency and cover of forb and cryptogams were higher on galleta-dominated areas than on needlegrass-dominated areas. These results imply a positive association between galleta and cryptogam cover, and a negative one between needlegrass and cryptogamic cover. However, the soil that supported galleta had a finer texture and a higher organic matter than that of the soil beneath the needlegrass cover, suggesting that galleta grass and cryptogams have the same habitat requirements.

In Australia, cryptogam cover has been both negatively (Eldridge 1993a) and positively (Graetz and Tongway 1986; Muncher et al. 1988) correlated to vascular plant biomass, but these reports indicate that detailed environmental factors must be considered. Given the many secondary products of lichens (Kershaw 1985), some lichen extracts probably suppress the growth of some species. In a Welsh greenhouse study, macerated (ground-up) tissue of *Peltigera canina* inhibited the root growth of five grass species by 2 to 80 percent depending on the species (Pyatt 1967). The water soluble secretion from *Peltigera* showed decreased inhibitory properties and root lengths were 60 percent or more of control plants (Pyatt 1967). In nature, maceration of tissue occurs only after heavy trampling or vehicular disturbance and in PJ woodland, *Peltigera canina* grows in the more mesic, shaded areas under the tree canopy where abundant grass is less likely; therefore, the ecological significance of the finding is unclear.

Consider the species specificity of inhibitory activity and perform field tests to determine their ecological significance. For direct relevance to range situations, test range plants with appropriate cryptogams. The effects of blue-green algae, lichen (predominantly *Collema*), and moss (*Tortula* and *Grimmia*) cover were tested on the establishment of three species of range plants (Harper and Marble 1988). Algal and lichen cover had a significantly positive affect on *Lepidium montanum* and *Sphaeralcea coccinea* but no statistically significant affect on *Elymus cinereus*. Moss cover had no affect on any of the three species. Field studies in Utah demonstrated that seedling establishment and survival of *Linum perenne L. Oryzopsis hymenoides*, *Sphaeralcea coccinea*, and *Elymus junceus* was significantly improved on cryptogamic surfaces rather than on scalped plots (Belnap 1992). A limited study determining the effects of moss litter on the germination of *Stipa thurberiana*, *Sitanion hystrix*, *Agropyron spicatum* showed moss litter *per se* had no unique properties (Schlatterer and Tisdale 1969).

Cryptogamic crusts are sometimes believed to form a barrier to seedling establishment (Harris et al. 1987; Hacker 1987). Cryptogamic crusts did not have negative effects on seed germination or seedling establishment of *Agropyron elongatum*, *Elymus junceus* or *Elymus cinereus* (St. Clair et al. 1984). In greenhouse studies where intact crusts were taken into controlled environments, seedling establishment of *Agropyron elongatum* and *Elymus junceus* was better on undisturbed cryptogamic crusts. This may have been due to the higher fertility of crusted soils. Also, there may be a difference between hummocked and flat cryptogamic surfaces (compare Figures 5 and 6). Hummocked surfaces provide more cracks and sheltered micro environments to promote seed germination (Hugie and Pasey 1964; Harper et al.

1965). The significance of soil surface morphology has been examined in a few studies (Eckhert et al. 1986a; Eckhert et al. 1986b). Four types of soil morphological types were examined in sagebrush communities of Nevada (Eckhert et al. 1986a). With the exception of sagebrush (*Artemisia tridentate*) emergence and survival of vascular plants was best on pinnacled and hummocked soil surfaces stabilized by cryptogams (Eckhert et al. 1986a).

Although juniper and pinyon interactions with terricolous cryptogams have not been explored, some inhibitory effects of lichens on conifers have been reported and investigation is needed. *Cladonia cristella* inhibited germination of *Pinus bankesiana* by about 60 percent (Brown 1967), *Cladina stellaris* suppressed seedlings of *Picea mariana* (Cowles 1982 in Harper and Marble 1988), and mats of *Cladonia alpestris* inhibited seedlings of *Pinus sylvestris* and *Picea abies* (Harper and Marble 1988).

Evidence indicates that a well-developed cryptogam crust influences below-ground microbial activity. In a comparison of soil under a *Collema*-cyanobacteria crust (commonly found in PJ woodlands) versus that under a bare surface, there were:

1. Greater vesicular-arbuscular mycorrhizal (fungi in symbiosis with certain plant families that increase root-absorbing capacity) associations with *Bromus tectorum*, *Coleogyne ramosissima* and *Festuca octoflora*;

2. Larger rhizosheaths (dense tangles of root hairs, root exudate, and bacteria capable of nitrogen fixation) on *Stipa hymenoides*; and

3. More abundant rhizobium (beneficial nitrogen-fixing symbiotic bacteria associated with legumes) with *Lupinus pusillus* (Harper and Pendleton 1993).

Modification of soil temperature, soil/plant water relations, and growth regulator factors are suggested as being involved.

Interactions with Fauna

Cryptogams provide a living crust and, after death and decay, provide organic matter to the soil (Kleiner and Harper 1972). This may be important to the nutritional and habitat requirements of soil fauna such as micro arthropods. Micro arthropods are important in maintaining a balanced ecosystem in PJ woodlands and it is essential that organic matter be available to them (Whitford 1991).

The full significance of cryptogams in the life cycles and food webs of either vertebrates or invertebrates is unknown and there are no studies in PJ woodlands. A subtle, but important, function of the cryptogamic crust may be its influence on vascular plant mineral content. Higher levels of some minerals have been found in plants growing in cryptogamic covered soil. Decline in the cryptogamic cover may result in mineral deficient plants, which would influence wildlife nutrition. For example, *Festuca octoflora* had a higher calcium and phosphorus content when growing in cryptogamic covered soil than when growing in bare soil (Harper and Pendleton 1993).

Some animals do not compensate for the low mineral content of vegetation by eating greater amounts of the deficient vegetable matter. For example, bobwhite quail were found to be calcium deficient because they did not consume enough of the calcium deficient vegetation to provide adequate calcium (Robbins 1983). In the Southwest, the decline of the desert tortoise has been associated with high levels of osteoporosis, a condition due to inadequate minerals in the diet (Harper and Pendleton 1993). Because the diet of the desert tortoise is at least 80 to 90 percent grasses and forbs (Hansen et al. 1976), it could become mineral deficient in areas where the cryptogamic crust has been destroyed (Harper and Pendleton 1993). Sodium is also an essential part of wildlife diet. Although sodium is widespread in the Southwest, its acquisition and retention may require some effort by herbivores (Robbins 1983). Licks are frequently provided to supplement the sodium intake of livestock but these are not appropriate for many smaller herbivores. Notably, desert stickleaf (*Mentzelia multiflora*) had a higher sodium content when associated with a cryptogamic cover. There are few known examples of mammals directly ingesting cryptogams as food. Lichens feature in the diet of reindeer (Pegau 1970) and fungi are an important source of calcium for fox squirrels (Robbins 1983).

Research on the interactions between birds and cryptogams is limited. Lichens are used by birds for camouflage, as material for nest building, and for food. A variety of birds (e.g., several species of vireo and hawk) selectively collect specific lichens

to build nests (Richardson and Young 1977). Complex ecosystem interactions such as these require further investigation in order to maintain a biologically diverse landscape.

CRYPTOGAMIC CRUST DISTURBANCE

Fire

There have been no direct studies of the effect of fire on cryptogamic crusts in PJ woodlands, but there have been numerous investigations in other closely related semi-arid ecosystems. Terricolous cryptogams of arid and semi-arid regions probably evolved without frequent fires because only relatively recently has wildfire become common in the semi-arid lands of North America (West 1990). Because readily combustible standing material is sparse, frequent natural fires are unusual where vascular plant cover is under 40 percent. Regions with over 40 percent vascular plant cover, especially those invaded by nonindigenous species (e.g., cheat grass) are more prone to fires in the dry season (Harper and Marble 1988).

Cryptogamic covers are damaged by fire, and the recovery rate apparently depends on the original community and cryptogam life form (Johansen et al. 1984; West and Hassan 1985; Callison et al. 1985). Generally, algae are the first to recover, while mosses and lichens are slower to re-establish. In a black brush community before burning, cryptogams contributed 9 percent to total cover, but after burning less than 1 percent. Even after 19.5 years there was little crust development on the burned plots (Callison et al. 1985). Cryptogam cover had not recovered two years after a burn in a sagebrush (*Artemisia tridentate*)-grassland community (West and Hassan 1985). In another sagebrush community, Johansen et al. (1982) reported that, although fire substantially decreased cryptogam biomass, viable algae were found three years after the burn with a species composition very similar to those in unburned sites. In a more mesic sagebrush shrub land, islands left after a major range fire were compared to the burned areas (Johansen et al. 1993). In both regions, algal propagules remained in the soil after the fire. Algae were mostly green in this area and recovery was relatively swift; taking place in the winter

months of the second year after the fire. Recovery followed vascular plant establishment, which suggests that a vascular canopy may be beneficial to algal crust development (Johansen et al. 1993). From field observations, it is likely that wet weather positively influences algal recovery after burning (Johansen 1984; Johansen et al. 1984; Johansen et al. 1993).

Fire frequency and soil conditions after a fire have received little research attention. Cryptogam cover was completely destroyed after a fire in a eucalypti woodland in Australia and recovery occurred after about four years (Greene et al. 1990). However, in the same area, increased fire frequency reduced the spatial distribution of the cryptogamic crust on the soil surface (Kinnell et al. 1990).

After fire in a greasewood-shadscale (*Sarcobatus vermiculatus-Atriplex confertifolia*) desert shrub community, greasewood predominated and cryptogam biomass was reduced significantly. However, the species composition of the algae remained essentially the same although the species proportions changed (Johansen et al. 1984). For example, *Nostoc commune* was more abundant in unburned than burned areas and other species of *Nostoc* were more common in burned than unburned sites. The functional significance of these observations is unknown. In this desert shrub community, algae recovered first and achieved full recovery within five years. Lichen and moss were slow to recolonize; after five years they had still not recovered. The first lichens to return were those with specialized asexual propagules containing both symbionts. *Collema tenax* was common in the unburned and burned areas. Within five years the only moss to recolonize in burned areas was *Pterygoneurum ovatum*, a species common on disturbed tracts of land and, in this particular study, rare on the unburned areas (Johansen et al. 1984). The relationship between fire temperature and rate of cryptogam recolonization has not been thoroughly explored. In PJ woodland there remains much to learn about fire and its affect on cryptogamic cover.

Grazing

Based on qualitative observations on the grasslands of Africa, hoof action has been described as

being important in maintaining a healthy grass-land (Savory and Parsons 1980; Steger 1982). Regardless of the type of plant cover and environmental conditions, this theory has been extrapolated to the Southwestern United States, including PJ woodlands, where there are typically thinner, more arid soils (Savory 1983; Savory 1988). Increasing evidence indicates that cryptogam destruction does not result in more grass cover. The consensus of many scientific studies is that cryptogam eradication produces more bare soil rather than increasing vascular cover, grasses or otherwise (e.g., Rogers and Lange 1971; Kleiner and Harper 1972; Kleiner and Harper 1977a; Kleiner and Harper 1977b; Brotherson et al. 1983; Jeffries and Klopatek 1987; Beymer and Klopatek 1992). The amount of damage caused to cryptogamic crusts by grazing is in proportion to the grazing pressure (Anderson et al. 1982a; Jeffries and Klopatek 1987; Rickard and Vaughan 1988; Beymer and Klopatek 1992). Mack and Thompson (1982) argued that large herbivorous ungulates are incompatible with maintenance of steppe where cryptogams, particularly crustose lichens, occupy a significant fraction of the soil surface.

Grazing also affects crust composition (Brotherson et al. 1983; Anderson et al. 1982b; Johansen and St. Clair 1986). In PJ communities, the cryptogamic cover in areas with long-term (40 years) grazing pressure was primarily composed of algae; moss and lichen components were rare (Brotherson et al. 1983). Apparently, no species of cryptogams behave like weedy vascular species, although some members of the blue-green algae and certain species of moss and lichen are better able to colonize disturbed land than other cryptogams. Reduction of cryptogam species diversity is also a consequence of grazing pressure (Kleiner and Harper 1972). Both vascular and cryptogam plants were heavily impacted by long-term (40 years) grazing in PJ woodlands (*P. edulis* and *J. osteosperma*) in northwestern Arizona (Brotherson et al. 1983). Overall, cryptogamic cover was reduced proportionally more than vascular cover; mosses and lichens were reduced by 85 percent and 83 percent respectively but, interestingly, both algal and grass cover were reduced by about 57 percent (Brotherson et al. 1983). Unfortunately, many range condition studies do not measure the cryptogamic cover although there have been

several suggestions that cryptogam cover could be used to assess range condition (Anderson et al 1982b; Klopatek 1991). Beymer and Klopatek (1992) reported that in a PJ woodland in Arizona, C3-grass cover was positively correlated to cryptogam cover. When grass cover was approximately 7 percent, cryptogam cover was 5 to 10 percent. Both life forms increased almost linearly up to a grass cover of about 20 percent and a cryptogam cover of approximately 22 percent (Figure 8). As grazing intensity increased, forb cover and bare ground increased and the visible cryptogamic crust declined (Beymer and Klopatek 1992).
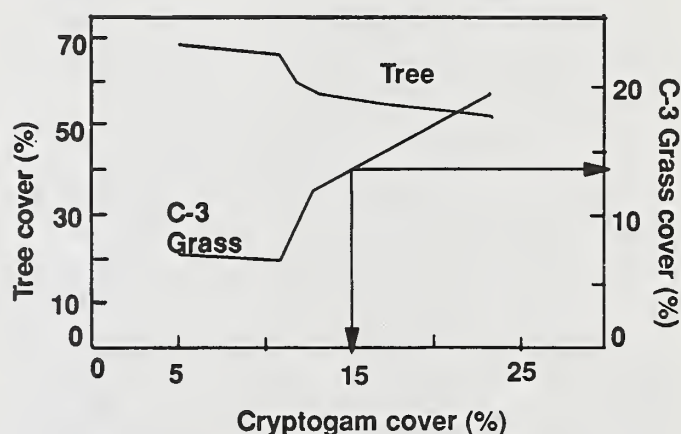
Figure 8. Relationship between C3 grass, cryptogam, and tree cover in pinyon-juniper woodland (Beymer and Klopatek 1992).

Recovery time from grazing varies between plant community types. In *Atriplex* communities in Utah, cryptogamic crust improved within 15 years of exclosure from grazing (Anderson et al. 1982a). In a comparison of seven- and twenty-year grazing exclosures (shadscale-greasewood communities), lichen, moss, and vascular plant cover was significantly less in the seven-year exclosure area (Johansen and St. Clair 1986). The extent of algal cover was similar in both exclosures but there were compositional differences. This implies that the seven-year exclosure site was still in the process of recovery and community development. Absence of a relic site precluded determination of whether the 20-year-old exclosure reflected full recovery. Neither cryptogamic nor herbaceous cover had recovered after ten years of rest from grazing in a black brush community in Utah (Jeffries and

Klopatek 1987). Observations that vegetation cover does not improve in PJ woodland and only slightly improves in other communities after seven years of grazing exclosure (Hughes 1983), demonstrates relatively long-term cover loss in these communities.

Platou and Tueller's (1985) excellent comparison of shrub-steppe (west of the Rocky Mountains) and prairie grassland (east of the Rocky Mountains) proposes that, although year-long, intermittent high-intensity grazing is incompatible with maintaining vascular plant cover in shrub-steppe zones, grazing is acceptable as long as complete rest is given during the growing season every few years to maintain bunch grasses. Johansen (1986) suggested that a rest period would favor cryptogam maintenance in the Great Basin areas. This recommendation may be equally valid for the similarly arid and semi-arid PJ woodlands.

Lichens have greater resistance to grazing mammals when wet (Pegau 1970) and cryptogamic crusts in the Southwest are most vulnerable to irreversible damage when dry (Harper and Marble 1988). Summer precipitation across most of the PJ range comes as short-duration, heavy downpours and the cryptogams remain moist for only short periods. For this reason, Anderson et al. (1982a) recommended against grazing on the ranges in the Great Basin of North America during the summer. Historically, the PJ woodlands were the primary rangeland for the larger herbivores (e.g., elk and deer) in the winter and spring when the cryptogamic crusts were more consistently moist (Hurst 1977; Mack and Thompson 1982).

In pastures in west central Utah, Marble and Harper (1989) compared the effect of seasonal timing on the degree of damage sustained to cryptogamic and vascular plant cover under heavy sheep grazing (17 sheep days/acre). There was a slight improvement in cover and a significant increase in species diversity when only early winter (Oct. 15 through Feb. 15) rather than half early- and half late-winter (Feb. 15 through May 15) grazing occurred. Additional support for early-winter grazing is in a study on saltbush/greasewood/sagebrush communities in western Colorado where early-winter grazing caused less runoff erosion than winter-long grazing (Oct. 15 to May 15) at the same intensity use (Lusby 1979a).

Apparently, protection of both cryptogam and grass cover may be compatible in the Great Basin

regions (Figure 9). Absence of grazing April 10 through July 1 benefits cool season grasses, warm season grasses benefit from grazing abstinence July 15 through Oct 15, and cryptogams tolerate animal impacts better in the winter (Watershed Management Practices for Pinyon-juniper Ecosystems 1992). Grazing October through February seems to be the least detrimental for both grasses and cryptogams. However, in parts of the PJ range where winters are generally dry (Pieper 1977), precipitation during all seasons permits cryptogams to be moist for only short periods. Therefore, apparently, any grazing in such regions would be detrimental to the cryptogam cover.

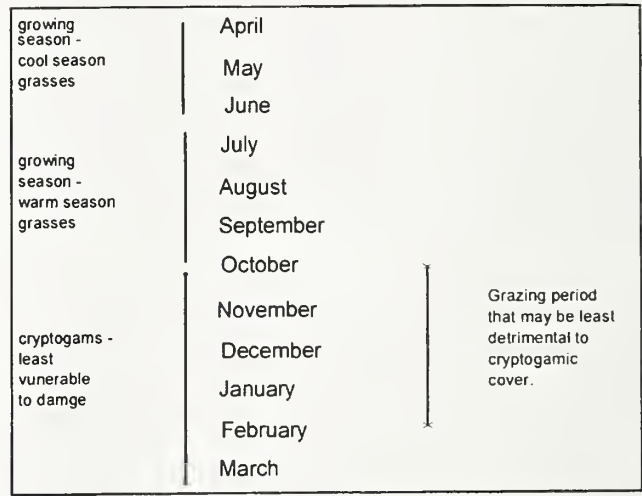On any grazing schedule, complete rest every few years during the winter and summer wet

Figure 9. Relative seasonal vulnerability of cryptogams to grazing in the Great Basin Region. Determining the impact of restricted, early winter, grazing on cover requires long-term evaluation.

seasons would promote buildup of algal numbers and permit maintenance of some diversity (Brotherson et al. 1983). In addition to seasonal fluctuations in abundance, there are seasonal species variation similar to the vascular plant seasonal variation (Johansen and Rushforth 1985; Johansen and Rushforth 1986; Johansen et al. 1993).

Trampling

Hikers and campers also cause severe disturbance (Cole 1990; Belnap et al. 1994). In controlled

trampling studies, using tennis shoes or lug-soled boots, in a PJ community with black brush (*Coleogyne ramosissima*) under-story, cryptogam cover was reduced to less than 50 percent after 15 passes and to zero after 250 passes (Cole 1990). The irregular, cryptogam-encrusted, aggregated soil surface became flat with loose sand that was easily eroded. The area occupied by the cryptogamic crust returned to pretrampling levels within five years, although the surface roughness (hummocking) did not re-establish, which indicates incomplete recovery (Cole 1990). The different soles caused no statistically significant differences. In Arches National Monument, cryptogam species diversity was considerably less in trampled areas (10 to 15 people/day for eight months/year) than on untrampled cryptogam covered sites; only one species of cyanobacteria was found in the trampled area (Belnap personal communication, with Ladyman). Compaction was five times greater in the trampled area and water infiltration rates were 90 percent lower than in untrampled areas. (Belnap personal communication, with Ladyman)

Vehicular traffic rapidly destroys cryptogamic crust (Johansen and Rushforth 1985; Belnap et al. 1994). In Utah, with adequate moisture from snow melt and absence of additional disturbance, algal hummocks can re-establish in jeep tracks within a year (Johansen and Rushforth 1985).

Pollution

Lichens (commonly saxicolous and epiphytic) are used as biological indicators of air pollution, especially in Europe (Nash 1976; Huckaby 1993). In polluted areas, changes in species composition occurs after morphology and physiology modification (Favali et al. 1991). Air pollution dramatically reduces species diversity (Wirth 1976).

Lichens (saxicolous, epiphytic, and terricolous) in the Four Corners region of the Southwest showed no significant changes in the local species composition or cover (a combination estimate of density and extent) after ten years of power plant operation (Marsh and Nash 1979). Possible reasons are:

1. Many of the lichens were crustose, which are the least susceptible to damage;

2. Lichens are most sensitive to sulfur dioxide when wet, therefore, the environment's

aridity reduced the amount of time that lichens were susceptible to injury; and

3. Ground-level sulfur dioxide levels are relatively low even when emissions are high (Marsh and Nash 1979).

Further studies on the effects of air pollution on cryptogams in the Southwestern United States are in progress (St. Clair et al. 1993).

CRYPTOGAMIC CRUST RECOVERY

Recovery Assessment

Recovery time depends on the disturbance type, the community structure, the soil, and the climate. Blue-green algae and some lichen species (e.g., *Collema tenax*) are relatively sturdy, but most lichens are fragile and recover slowly. Recovery rates depend on moisture availability (Johansen 1984; Johansen et al 1993). All life forms in cryptogamic crusts recover quicker with substantial precipitation. Temperature is also important; different species of cryptogams have different optimum temperatures for growth (Johansen and Rushforth 1985). Recovery from fire and grazing is difficult to predict. In *Atriplex* and/or greasewood communities, cryptogamic crust improved 15 to 20 years after grazing exclosure (Anderson et al. 1982a; Johansen and St. Clair 1986). Similarly, cryptogamic cover re-established on a disturbed bare surface in a badly eroded area in Australia after 15 years (Muncher et al 1988). In Utah, 20 years after fire in a black brush (*Coleogyne ramosissima*) community, there was no cryptogamic crust recovery (Callison et al. 1985). In a similar community, algal recovery was estimated at 40 years, lichen recovery at 45 to 85 years, and moss recovery at about 250 years (assuming a linear accumulation rate equivalent to that being observed over the two-to-five year study period; Belnap 1993).

Algae can multiply and grow relatively rapidly, but lichen growth is much slower. Segments of lichen podentia have taken at least two years to initiate new growth after shattering. The annual growth rate of *Cladonia* species of lichen was reported at 5 mm per year (Pegau 1970). In contrast, the maximum distance traveled on solid agar by filaments of *Microcoleus vaginatus* during a 12-hour period of light was 4.8 cm (Campbell 1979).

This corresponds to approximately 500 times the length of the fastest filament and provides a measure of the potential for mat expansion in nature via filament motility. Algal crust is formed by filament multiplication and sheath production, which is continually produced and abandoned while migrating (Campbell 1979; Belnap 1992).

Recovery assessment methods require refinement. Visual assessment of crust recovery by estimating area coverage alone may not be completely accurate. The contribution of unicellular algae to crust formation and the thickness of the crust is often difficult to judge. Chlorophyll *a* concentrations have been used as a measure of photosynthetic capacity and thus physiological activity, as well as an indicator of biomass. Chlorophyll *a* levels are sensitive guides to algal recovery (Belnap 1993) and have been well correlated to biomass (Beymer and Klopatek 1992), soil cryptogam status (Klopatek and Thomas 1994), and algal cell density (Ashley and Rayburn 1994). However, chlorophyll *a* concentration does not fully reflect the organism's physiological status and is not the only basis for a measure of potential photosynthetic activity. The abundance of antennae pigments are just as important (Beymer and Klopatek 1991) but no techniques have yet been developed to use them to accurately assess recovery. In some studies chlorophyll *a* and visual estimates do not distinguish between disturbed and undisturbed plots (Belnap et al. 1994) whereas nitrogenase activity does. (Belnap et al. 1994). Nitrogenase activity declined dramatically in disturbed areas and remained less than 20 percent of undisturbed levels for nine months after trampling, raking, scalping and vehicular traffic (Belnap et al. 1994). Therefore, nitrogenase activity is probably the most sensitive indicator of algal recovery.

However, visual assessment by estimating cover remains the most rapid method and, although there may be an overestimate of cover using visual assessment, there is good correlation (r^2=0.92) with chlorophyll *a* methods (Beymer and Klopatek 1992). Chlorophyll *a* was reduced from 9.9 mg chlorophyll/cm^2 on ungrazed land to 3.1 mg chlorophyll/cm^2 on grazed land and respective visual cover estimates were 23.3 percent compared to 5.2 percent (Beymer and Klopatek 1992). Grondin and Johansen (1993) noted substantial microscale heterogeneity in algal abundance in PJ woodlands in Colorado and, regardless of the assessment method applied (e.g.,

chlorophyll *a* or direct counting), recommended taking a composite of small samples when quantifying the algae in cryptogamic cover.

A very important aspect of recovery to a cryptogamic crust is the hummocked, pinnacled topography, rather than only the degree of visual blackness. Flat surface crusting of cryptogamic cover is usually an early stage of development; therefore, when considering recovery, estimating the degree of topographic roughness is important. An interesting observation by Johansen and Rushforth (1985) was that hummocking could occur relatively quickly; greater hummocking was obvious in May after a snow melt than in the previous fall.

Inoculants

Inoculation with cryptogam preparations has been proposed as one way to hasten cryptogamic crust development after disturbance (St. Clair et al. 1984; Belnap 1993). Although lichen and moss growth tends to be slow (Kershaw 1985), algae have the potential for rapid recolonization using inoculation preparations (Campbell 1979).

This approach was tested by St. Clair and Johansen (1985) and St. Clair et al. (1986) in the following study. Fire destroyed much of the vegetation in a shadscale-greasewood community on a valley floor and in a PJ community on drainage slopes. Most of the burn area was used for grazing and it was reseeded after the fire using standard stabilization techniques. However, in the following year several drainage areas were not effectively stabilized and test plots were established within troublesome sloping drainages. These were inoculated with one of three amendments; soil crust (terricolous algae, diatoms, *Collema tenax*)-water slurry, subsoil surface-water slurry, and water only. The plots treated with soil crust-water slurry showed much higher numbers of algae, diatoms and even *Collema tenax* after six months. However, climatic conditions were especially favorable (i.e., moist) and such rapid establishment may be unusual.

Dry inoculation (crumbling material from one area and spreading it as thinly and evenly as possible over another area) was made over scalped gypsi-ferous and sandy substrates in eastern Utah (Belnap 1993). After two years the inoculated plots had more algae, lichen, and moss cover than uninoculated plots, but still had much less than the undisturbed control sites.

Delivering inoculants with cultured algae to help keep crusts intact is being tested (Buttars et al. 1994; Johansen et al. 1994). Pellets of cultured cyanobacteria were made using alginate to avoid using the slurry technique, which requires large amounts of water. In greenhouse studies this approach had limited success, partly because the algae could not escape from the pellets (Buttars et al. 1994). Preliminary data suggests that using crushed pellets of cyanobacteria dried on the surface is a more effective delivery method (Buttars et al. 1994). Field plots were established in a greasewood-shadscale community in 1993 in support of these greenhouse trials and are still in progress (Johansen et al. 1994).

Inoculation techniques have been studied in other countries. In the late 1940s Singh (1950) successfully reclaimed alkaline lands in India on which plants, including crops, were failing. In this case the field conditions were very wet because the inoculations coincided with the end of the monsoon season. Considering the benefits of moisture on cryptogam development (Klopatek and Thomas 1994), inoculations in the Southwest United States would be most beneficial in the fall; recovery would then coincide with the early spring. Stabilization of waste-sand tips, made during quarrying activities, and their subsequent improved water holding capacity was achieved in Cornwall, England using the algae, *Microspora amoena* (Mackenzie and Pearson 1979).

Relying on pre-existing crusts for rehabilitation work defeats the long-term objectives of increasing overall cryptogamic cover. Therefore, future work on artificially growing cryptogams and using inoculant technology is essential. Algae successfully multiplies in vats (Borowitzka and Borowitzka 1988; Lembi and Waaland 1988) and the technology exists to manipulate and grow mosses (Goode et al. 1992) and lichens (Yoshimura et al. 1993) in culture. Therefore, in the future, appropriate inoculants may be available.

SUMMARY AND FUTURE RESEARCH

Cryptogamic crust:

1. Provides soil structure by causing soil particle aggregation that retards erosion caused by precipitation and wind;

2. Adds organic matter and nitrogen to the soil;

3. Can be nutritionally beneficial to adjacent vascular plants;

4. Provides suitable habitat for certain species of endemic plants; and

5. May also influence wildlife nutrition.

There is valid evidence that cryptogams occupy land that would otherwise be bare; and that they do not compete with grass.

Grazing during dry conditions is especially damaging to cryptogamic cover. Fire is also destructive. After disturbance:

1. Recolonization by algae is relatively rapid (within five years);

2. Mosses and lichens are relatively slow to recover (15 to 200 years); and

3. Species diversity declines.

Cryptogamic crusts in the PJ communities have two types of morphology, relatively flat with frequent surface cracks, or pinnacled and hummocked surfaces. The physiological and ecological functions (i.e., nitrogen fixation and soil stabilization) of the more mature, rough surfaces are better developed than the flat surfaces.

There remains much to discover about the physiology, function, and composition of cryptogamic soil crusts. Our understanding of the interactions between different plant communities, plant species, soil types, and cryptogam species is still in its infancy. What defines recovery of cryptogamic crusts in different environments and what is the most appropriate measure (number of individuals, species diversity, extent of physiological activity) is evolving.

How cryptogams can best be used to rehabilitate disturbed and degraded land requires more study. Should seeds of compatible vascular species be distributed with the cryptogam inoculum? Does crust age affects its durability and longevity, influence its ability to stabilize soil and affect the germination and growth of vascular plants? Are younger crusts more likely to suffer storm damage? If so, is this because they are thin, not as aggregated, or not as species diverse?

Determining what species of cryptogams develop stabilizing crusts on south-facing slopes is

an important area of investigation. However, in the quest for reliable and effective cryptogams to colonize troublesome areas, introduction of exotic species should be avoided, in case they behave as weeds and cause future ecological problems. In the Southwestern United States, cryptogamic crusts require careful study to determine how to manage them along with grazing pressures. Although grazing causes long-term damage to cryptogamic crusts, alternative grazing strategies may exist to lessen the impact, and help sustain crusts and their benefits in the ecosystem.

West (1990) stated that additional research is required before cryptogamic crust protection is warranted. However, this review suggests that, although more research is essential, there is a sufficient amount of quantitative evidence indicating that cryptogamic crusts perform important ecological functions, particularly in soil stabilization and nutrient cycling in the Southwestern United States. Management of cryptogamic crusts is complex because of long recovery times and the species loss potential following disturbance. Yet, long-term sustainable management of PJ woodland requires careful consideration of the role of cryptogams in the ecosystem.

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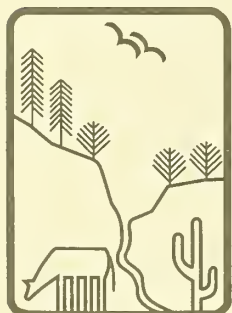
Rocky Mountains

Southwest

Great Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526